Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

THE

AMERICAN NATURALIST.

VOL. XXXVIII. *May, 1904.* NO. 449.

THE ANATOMY OF THE NORTH AMERICAN CONIFERALES TOGETHER WITH CERTAIN EXOTIC SPECIES FROM JAPAN AND AUSTRALASIA.

(*Continued from page 273*).

D. P. PENHALLOW.

THE MEDULLARY RAYS.

THE medullary ray, in the various details of its structure as presented radially and tangentially, comprises some of the most important features for diagnostic and taxonomic purposes. While it presents numerous variations, these are, in the main, of such a nature as to give them very positive value for both generic and specific differentiations. Primarily the medullary rays are to be regarded as a residue of the original fundamental structure which has been left over in the genesis of the primary stele, but they are capable of reproduction or extension under the influence of the cambium in the course of secondary growth. In all such cases, however, they are typically composed of the same elements which are necessarily parenchymatous. Deviations from this structure may arise through the introduction of other elements, but such alterations always arise in a manner which indicates their relation to the evolution of higher types of organization. The ray presents few features of value in the transverse section, and these will be sufficiently dealt with in the systematic portion[1] to make further reference to them at this time unnecessary. It only remains to point out that those rays in the Abietineæ which contain resin canals, and which present an unusual width, possess no special diagnostic value in this plane of section.

Radial Section.— Viewed radially, the medullary ray is seen

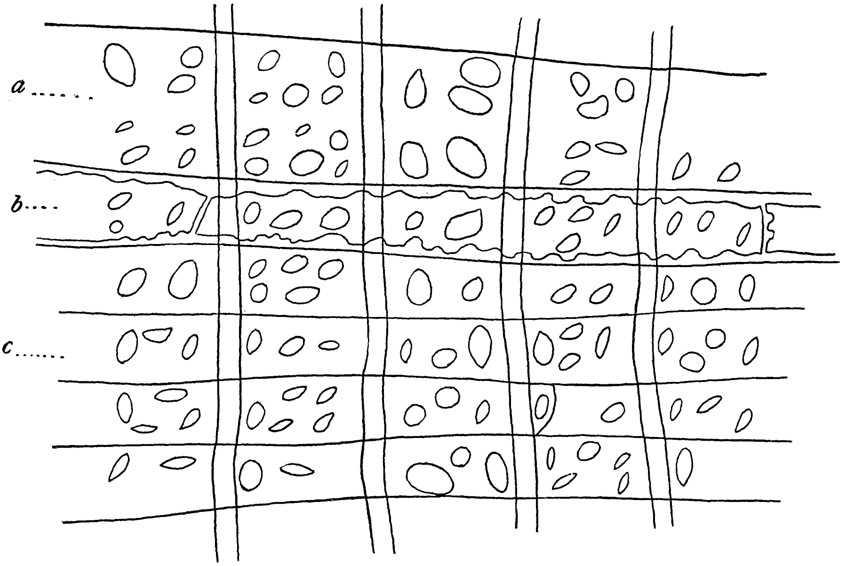


FIG. 17.— *Pinus palustris.* Radial section of a medullary ray showing characteristic pits on the lateral walls. *a*, a thin wall broken out; *b*, thick-walled parenchyma; and *c*, thin-walled parenchyma cells. × 280.

to be composed of a series of cells extended in a radial direction and superimposed so as to form a muriform band from one to many cells in height. In general terms, the higher the ray the lower the component elements, from which it follows that in one-celled rays the cells are usually highest; but this feature is only of general interest since it rarely has a bearing upon the chief questions at issue. In some cases two structural types may be recognized — the one containing resin passages, the other devoid of such structures. Where such passages occur the structure of the ray shows a variation of detail which makes it of no value for diagnostic purposes, and it is therefore eliminated from the following discussion.

---

[1] The systematic portion here referred to, constituting Part II of the present series, will appear in the *Transactions of the Royal Society of Canada* for 1904.

A feature of primary importance in the constitution of the ray is the occurrence of two kinds of parenchyma cells. In 95% of the genera the upper and lower walls are always thickened by secondary growth and more or less strongly perforated by simple pits (Figs. 17*b*, 21 and 23). This feature also applies to 56.1 % of the genus Pinus. It possesses no special value for either specific or generic differentiations except so far as it applies to cells which are markedly different and justify the special terms "thick-walled" and "thin-walled." It is obvious, then, that the thick-walled cell is to be regarded as the normal structure for the ray of the Coniferales as a whole, while the thin-walled represents the exceptional form which is introduced in response to some special demands. Although the thick-walled cells occur in the genus Pinus to the extent of 56 %, they show a diminishing frequency, eventually becoming rare and ultimately replaced by thin-walled cells. Reference to them in the following diagnoses is always specified by (1). In 43.9 % of the genus the upper and lower walls are thin and absolutely devoid of pits. For diagnostic purposes such cells are always referred to as (2). In some cases they are so undeveloped as to be obscure and readily broken out in the process of section cutting, so that they are often entirely wanting (Fig. 17 *a*). Such thin-walled cells are typically developed in *P. palustris*, *P. tæda*, etc., and it is to be observed that they are always associated with the highest forms of development. Transition forms occur. These are first seen in the soft pines where occasional thin-walled cells, devoid of pits, are interspersed and often coterminous with the thick-walled elements. In the hard pines the same relation exists, but it is gradually reversed until the thin-walled cells altogether predominate. Such gradations are exhibited in *P. coulteri*, *P. jeffreyi*, *P. pungens*, *P. tæda*, *P. cubensis* and *P. inops*, and they afford evidence of value as to the sequence in development of the species. In *P. murrayana*, *P. cubensis* and

P. insignis the transition forms exhibit much more detailed gradations by virtue of which it is often exceedingly difficult to distinguish between the two forms of cell, since whether coterminous or parallel the variations in thickness change in such a way that the one type passes gradually into the other. When these variations are viewed collectively and taken together with the general fact that the thin-walled cells are a feature of the higher types of organization, we may reasonably conclude that the thin-walled cells have been derived from the thick-walled through a process of arrested development. The cause of such alterations is to be sought for, and it will doubtless be found in connection with another component of the ray.

The terminal walls of the ray cells present three typical variations: (1) thin-walled and entire; (2) thin-walled and locally thickened, and (3) thick-walled and coarsely pitted (see table, D of anatomical data). The first feature is a characteristic of 52.6 % of all the genera, inclusive of Ginkgo, from Agathis to Sequoia, while it also appears in Cupressus and Abies in part as exceptional, and in the genus Pinus to the extent of 85.3%. The wall presents no secondary growth in thickness, either locally or generally. In the majority of cases it crosses the line of the principal cell axis either at right angles or diagonally,

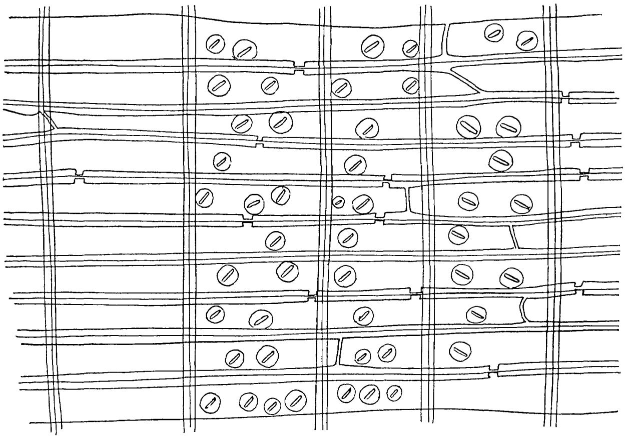


FIG. 18.— *Taxodium distichum.* Medullary ray showing the structure and position of the pits on the lateral walls; the straight ray cells and the thin, straight, terminal walls. × 280.

features which are usually of very secondary value, although in a few cases, as Taxodium, it may serve a useful purpose as an associated character, for differentiation from closely allied genera (Fig. 18). In other cases the wall is more or less strongly curved. This feature is prominent in Thuya, Cupressus, Podocarpus, Thujopsis and Cryptomeria, as also in the more highly developed hard pines. To a less extent it also occurs in Taxodium, and it constitutes a character of some value for differential purposes (Fig. 19).

The second variant differs from the first in that the otherwise thin wall is locally thickened (Fig. 20), the secondary growth forming one or more beaded enlargements. This is a feature which occurs exceptionally in Abies, Pseudotsuga, Picea and Pinus, but it is typical in Cupressus (66.0 %) and Juniperus (72.7 %) where it constitutes a diagnostic element of great value. It is in all cases, however, to be regarded as a transitional form between the first and the third variants, and from this point of view it also possesses a somewhat definite phylogenetic value. The third variant is characterized by a marked general, secondary growth of the wall, which thereby becomes more or less strongly thickened and traversed by numerous simple pits (Fig. 21). It occurs exceptionally in Juniperus and Pinus, but it is typical in Abies (90.9 %), Tsuga (100.0 %), Larix (100.0 %) and Picea (90.0 %). In Abies and Juniperus, where transitional forms sometimes occur, the walls in the spring wood may be

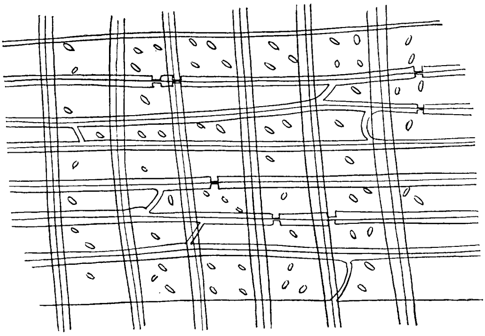


FIG. 19.— *Thuya gigantea.* Medullary ray showing the form and disposition of the pits on the lateral walls; the thin and curved terminal walls; the cells contracted at the ends. × 280.

only locally thickened, but in such cases the typical feature always appears in the summer wood where such secondary alterations are most strongly emphasized.

For taxonomic purposes, such features possess a definite value. The thick-walled cells of Tsuga, Larix and Picea permit of an easy and definite segregation of these three genera in those cases which otherwise might involve a strong element of doubt, and the same rule holds true, though to a less extent, with respect to the locally thickened walls in Cupressus and related genera.

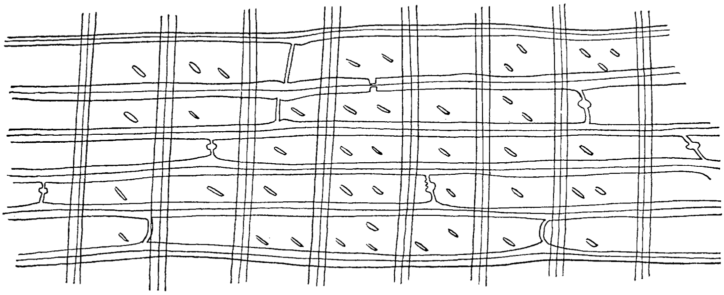


FIG. 20.— *Cupressus macnabiana.* Medullary ray showing the form and position of the pits; the thin, curved and locally thickened terminal walls. × 280.

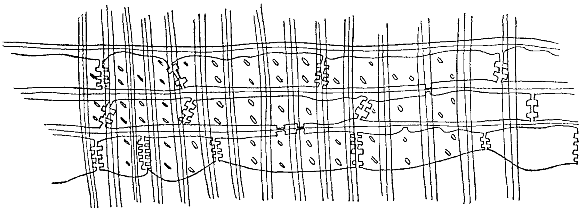


FIG. 21.—*Juniperus occidentalis.* Medullary ray showing the form and disposition of the pits on the lateral walls; the thick and coarsely pitted terminal walls. × 280.

Pits on the lateral walls of the ray cells are an invariable feature of all investigated species of Ginkgoales and Coniferales, including fossil representatives and the Cordaitales. They vary very much in form, size and number. In such types as Juniperus, they are most diminutive (Fig. 21) and generally numerous, while in many of the pines, such as *P. resinosa*, *P. koraiensis* or *P. reflexa* (Fig. 22) they attain to maximum size and occupy nearly the entire surface of the wall within the limits of a wood tracheid, thereby becoming few in number. In Sequoia (Fig. 23) or Taxodium (Fig. 18) they are typically oval; in *Pinus cubensis* or *P. tæda* (Fig. 24), they are variously lenticular, while in *P. resinosa* or *P. koraiensis* they are oval or oblong, or even quadrangular. Such variations as a whole, are far more numerous and sharply defined in Pinus than in any other genus known. In all the investigated genera, the pit is bordered. This finds either partial or complete exceptions in the genus Pinus to the extent of 78.1 % of the species, in which the pits are either simple throughout, or they exhibit a more or less definite border in the summer wood only. That a border is a characteristic feature of fossil representatives, is justified by comparison with existing species, but it is not always recognizable in consequence of the alterations of structure due to the general process of petrifaction. Such obliteration not infrequently involves the pit orifice also. It is thus apparent that such structures often fail in the determination of fossils. In existing species the border is often so faintly defined as to be difficult of recognition, and this is especially the case in rays of a resinous character. In all such cases, however, the requirements of a correct diagnosis are fully met by the pit orifice. The general law of development then, is such that all genera except Pinus may be held to be characterized by bordered pits.

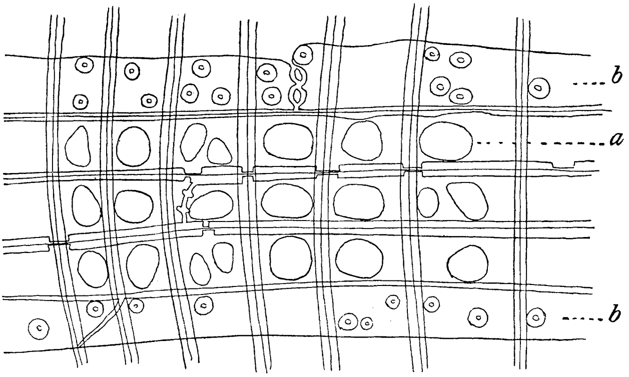


FIG. 22.—*Pinus reflexa.* Medullary ray showing (*a*) the form and disposition of the pits on the lateral walls; (*b*) the ray tracheids. × 280.

Their strong tendency to obliteration in that genus is found to coincide with the more marked development of ray tracheids which undoubtedly assume more completely the original functions of the parenchyma cells, these latter in consequence, suffering constant structural reduction, as in the hard pines.

In the distribution of the pits an important feature appears in the numerical variation in different parts of the ray. For diagnostic purposes it is necessary to have reference to the number of pits, not upon the entire surface of an individual cell, but within the limits of a spring or summer tracheid as the case may be. They are invariably most numerous in the region of the earliest spring tracheids, usually diminishing toward the summer wood where the change may sometimes take place abruptly, and in which they are most commonly reduced to one with occasional obliteration in the most highly modified tracheids last formed. A similar law of distribution is applicable within the vertical limits of the ray. When these structures are several cells in height, the number of pits is typical, and, within certain narrow limits, constant for all except the marginal cells. Thus if the normal number is 1–2 for the central cells, it may sometimes rise to 4, 6 or 8 in the marginal cells only, and such exceptions must be noted in diagnosis. When the ray is only one cell in height, the number of pits agrees with that for the marginal cells. Such numerical variations possess but little value for generic purposes, but as a specific character they may be held to constitute the principal differential feature in the last analysis. These relations are expressed typically in the genus Sequoia, the two species of which may be definitely differentiated. *S. gigantea* is characterized by oval and commonly narrowly

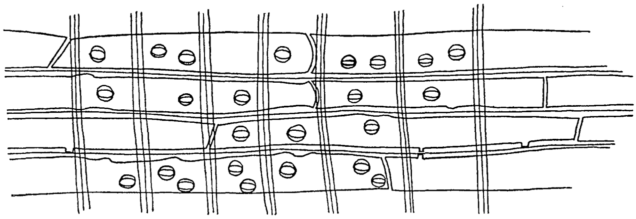


FIG. 23.—*Sequoia gigantea.* Medullary ray showing the form and disposition of the pits on the lateral walls. × 280.

bordered pits, the broadly oblong orifice equal to the outer limits of the pit and chiefly parallel with the cell axis, 1–2, more rarely 3–4 per tracheid. In somewhat sharp and definite contrast to this, *S. sempervirens* has large, oval, narrowly bordered pits, 2–6 per tracheid, the round or broadly oblong orifice either parallel with or diagonal to the cell axis. In Libocedrus the pits are small, narrowly bordered, oval, with a lenticular, diagonal orifice, 1–4 per tracheid. Or again in *Larix americana*, the pits are "2–6 per tracheid becoming distinctly smaller toward the summer wood where they are abruptly reduced to 2, and finally 1 per tracheid." In *Cupressus pisifera* the pits are "chiefly 2 in radial series, or in the marginal cells and low rays upwards of 6 per tracheid." In *Taxodium distichum* the pits are round, conspicuously bordered and large, with a very narrowly lenticular and diagonal orifice which is often as long as the outer limits of the pit. But in the analytical key it will be observed that this genus is naturally brought into close relations with Sequoia which is also distinguished by large, bordered pits. The ultimate differentiation then rests upon the fact that in the latter, the pits are *oval*, the border often *narrow*, sometimes *obscure*, while the *olbong or* lenticular, usually rather broad orifice is generally parallel with the cell axis. As a final illustration the four pits of *Pinus monophylla*, or the 1–5 throughout,

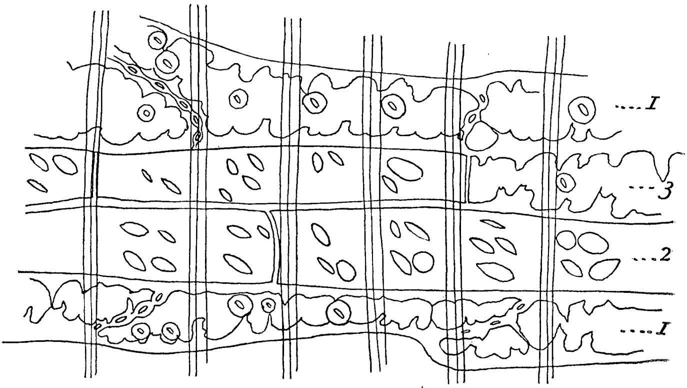


FIG. 24.—*Pinus serotina*. Medullary ray showing (*1*) the ray tracheids with dentate walls, (*2*) the structure of the parenchyma cells, (*3*) tracheids coterminous with parenchyma cells. × 280.

finally reduced to 1–2 in the summer wood of *P. balfouriana*, point with much definiteness to these particular species, while among the hard pines the occurrence of large, oval or squarish pits, 1 or rarely 2 per tracheid, segregates a group of four species. Detailed as these features are, they are not accidental, but of such constancy as to admit of no hesitation in accepting the conclusions to which they point.

The length of the ray cell is subject to considerable variation, not only within the limits of an individual, but as between one species and another. Our studies, however, do not permit the formulation of a law applicable to specific differentiations, even if such a law does exist, which present evidence leads us to doubt; but details of length, in terms of spring tracheids, have been incorporated in all the diagnoses, since they are often very suggestive and thus may assist in the ultimate recognition of the species.

The form of the cell is of more evident value, although too much stress must not be laid upon it. The cell is either straight, as in Juniperus, Libocedrus or Picea (Fig. 21), or it becomes fusiform through contraction of the extremities as in Cupressus, Sequoia, Taxodium, etc. (Fig. 19). As a well defined differential character its value is only one degree higher than the length of the cell, and it has been introduced into the diagnoses for the same reason as a controlling factor of secondary importance.

In the higher Coniferæ the medullary ray is distinguished by the presence of an element which differs materially in its structure from the associated parenchyma cells. These elements have been designated by De Bary (9, pp. 491–492), as "ray tracheids." Their structure is so peculiar, and they present such important relations to classification and development, as to necessitate a somewhat detailed account of them, to some extent in recapitulation of well known observations by De Bary (9, p. 491) Hartig (19, p. 13) and Göppert (17).

As stated by De Bary, the ray tracheid resembles the parenchyma cells, from which they differ, however, in the presence of bordered pits on *all* their walls. Furthermore, such pits not only differ materially in form and size from the bordered pits of adjacent parenchyma cells, but they are always much smaller than the pits of those wood tracheids on which they border. Such tracheids are invariable features of the ray in all the higher Coniferæ from Tsuga and Pseudotsuga to Pinus to the extent of 25% of the investigated genera. In Juniperus they occur very rarely, being found, so far as I am aware, in only one species (*J. nana*) out of a total of eleven, and they are so sparingly developed as to readily escape observation. In Thuya they are to be met with in *T. japonica*, likewise in a rudimentary state of development. Out of nine species of Cupressus they occur only in *C. nootkatensis*. Of the ten investigated species of Abies, they are found only in *A. balsamea*. In commenting upon this fact many years since, De Bary (9, p. 490), also pointed out that among European species *A. excelsa* is similarly exceptional, but no attempt has been made to interpret their significance. In Thuya, Cupressus and Abies the tracheids are strictly marginal in the composite rays, forming the entire structure in rays only one or two elements high. This relation obtains in all the higher Coniferæ in the first instance; but in Larix, Picea and Pinus, where there is a notable increase in numbers, they also become interspersed with the parenchyma cells and eventually predominate over them, a feature which is especially characteristic of the hard pines. Efforts have been made to show that in all such cases the two kinds of elements succeed one another in a definite order from above downward — or the reverse — but our studies have failed to show that this is capable of practical application to the purposes of classification, or even of phylogeny (9, p. 491). The great fact of importance for our present purpose, however, and one which stands out with much prominence, is that the ray tracheids are not a structural feature of the more primitive Coniferales, but only of the higher types such as Picea and Pinus. Furthermore, the primitive position for these structures is in the one or two-celled rays, or correspondingly in the margins of the composite rays.

In Thuya and Cupressus the tracheids appear to stand by themselves, and they exhibit no special relations to the parenchyma elements which would permit of inferences as to their possible origin. In the genus Pinus, on the other hand, where the relations are somewhat complex, evidence does appear of such a nature as to suggest their derivation. In *Pinus inops*, *P. torreyana*, *P. pungens*, *P. clausa*, *P. tæda*, *P. palustris* and *P. cubensis*, we frequently find thick-walled parenchyma cells and characteristic ray tracheids coterminous with one another. This does not mean a simple association, since in nearly all such cases, as typically presented by *P. palustris*, they also show a graduated structure of such a nature as to confirm the belief that the one passes into the other by structural gradations. That such is the case cannot be doubted, and if further confirmation were needed it is afforded by the precisely parallel relations to be met with in the formation of resin cells and resin canals. A further fact of much significance from the standpoint of development, is that such interchangeable relations are peculiar to the highest types of the genus Pinus. But we may ask, what is the function of these structures which make their appearance only in the higher Coniferæ; what is the proper significance of their appearance there, and do any other plants offer parallel examples?

In the so-called medullary rays of *Lepidodendron selaginoides* (49, p. 141) there are numerous reticulated or spiral elements which are undoubtedly of the nature of tracheids, and they may be held to represent the ancestral form of the ray tracheids in the Coniferæ, toward which they bear the same relation that exists between the spiral protoxylem element and the characteristic wood tracheid with bordered pits. From this it is apparent that the ray tracheid of Pinus or Tsuga represents a primitive structure which reappears in response to conditions of growth and structural alterations of such a nature as to demand the interposition of more simple, because more primitive, elements for the proper performance of necessary functional activities. These activities, in the case of Lepidodendron, are probably expressed in the radial distribution of water (51, p. 141), and we are no doubt correct in assuming similar activities to be carried on in the higher Coniferæ. In all those species which present the primitive structure of the thin-walled ray cells, both fossil and recent, there are no tracheids to be found. As a tendency to thickening of the wall arises, there is also developed a sporadic tendency to the development of ray tracheids as in Thuya and Cupressus. It is also a noteworthy fact that simultaneously with a general thickening of all the cell walls throughout the ray, as in the genus Tsuga, ray tracheids become a constant and prominent structural feature. This relation exists in Pseudotsuga, Larix, Picea and Pinus, and it is a remarkable fact that as the type of organization advances, and the structural modifications of the wall become more profound, the tracheids gain steadily in numbers and importance until they finally replace the parenchyma cells more or less completely. Such facts serve to direct attention to the idea that by such progressive alterations the ray cells gradually lose their normal functional powers with respect to the radial distribution of water, and under such circumstances it is imperatively demanded that this deficiency should be met through some other structures. Under these circumstances two alternatives are possible. First, that the thick-walled and useless cells should return to their primitive condition in opposition to the general course of development, and once more resume their appropriate functions. Such structural reductions do in reality occur in these very cases, as shown in *Pinus tæda*, etc., but it is to be observed that they are of the nature of a growth which has been arrested at such an early stage as to be devoid of many of the normal structural features. Furthermore, it would be difficult, if not impossible, to obtain evidence from other plants in support of a hypothesis of this nature. It is true that in the case of girdled pines the heart wood may resume an activity long since lost, and thus take upon itself once more the function of the sap wood, as also to some extent the function of the bark, but such renewed functional power does not in any way involve structural modifications of existing elements, and cases of this sort cannot be cited in support of the hypothesis stated. Under these circumstances, therefore, it is fair to conclude that such arrested development expresses diversion of energy to the preponderant tracheids.

The second alternative permits us to consider that in the ordinary course of development the ray cells gradually lose their functional activity as a result of extreme structural modification, and that this loss of power cannot be restored, even though the wall may return to a primitive condition of structure through various phases of atrophy. In accordance with this idea the tracheid would be introduced as the most natural because the original medium for such activities as are centered in the ray, and it would therefore acquire additional importance both numerically and functionally in direct proportion to the loss of power experienced by the parenchyma cells. This appears to be a reasonable interpretation, and in the light of observed facts it would seem to be the correct one.

A structural feature of great importance in the ray tracheid appears in certain inequalities of the upper and lower walls which take the form of teeth-like projections into the cavity (Fig. 24). In what may be regarded as the most highly developed tracheids the teeth project across the cell cavity until they meet and coalesce, thereby forming a more or less definite reticulation which gives to the tracheid a very characteristic appearance. As seen in tangential section, such reticulations often appear as narrow bands crossing the cavity from side to side, thus giving the cell a varying aspect. Such dentate and reticulated tracheids are absolutely confined to the second section of the genus Pinus, in which they constitute one of the most characteristic features to the extent of 68.3 % of the species. A more detailed analysis of this feature, as applied to the hard pines, is desirable. In *P. resinosa* and *P. thunbergii*, the tracheids are simply dentate. In six species represented by *P. murrayana* the teeth extend into definite reticulations confined to the summer wood; but in six other species represented by *P. jeffreyi*, such reticulations are sparingly developed throughout the ray. In *P. tæda* a transitional form appears. Typically this species shows the tracheids to be sparingly reticulated, but occasionally they are strongly reticulated throughout. This brings to mind the further fact that in all species which are sparingly reticulated there is a marked tendency to strong reticulation in the summer wood. In the thirteen remaining species the tracheids are uniformly strongly reticulated throughout the extent of the ray, and this feature attains its highest expression in *P. palustris* and *P. cubensis*. It is therefore manifest that we have to deal here with a graduated development of such a nature that the simply dentate tracheid is the most rudimentary, while the strongly reticulated is of the most advanced type of structure.

The value of the ray tracheid for taxonomic purposes depends upon: (1) its occurrence in certain genera, and (2) its structural peculiarities. The simple wall of the tracheid, in the great majority of cases, affords no basis of specific differentiation, but in the various forms of dentate and reticulated walls of the second section of Pinus, it is of well defined value in this respect. *Pinus resinosa*, *P. thunbergii* and *P. koraiensis* are all characterized by the occurrence of simple teeth which are sometimes sparingly developed. This feature is intimately associated with the occurrence of large, simple and single pits on the lateral walls of the ray cells. From this group *P. densiflora* may be differentiated by the reticulations in the tracheids of the summer wood. Among the hard pines, *P. tæda* is distinguished by ray tracheids which are typically sparingly reticulated throughout, but on the other hand, *P. palustris* and *P. cubensis*, which probably represent the highest types of the genus, are at once separated from all other species by reason of the extent to which reticulations are developed.

The relations which the tracheids bear to the parenchyma cells in the general composition of the ray also have an important bearing upon specific differentiations. In the genus Tsuga the tracheids are sometimes interspersed, affording the first instance of a relation which later becomes most prominent in the higher genera, and the same relation is also expressed in Pseudotsuga and Larix. In Picea there is a somewhat stronger tendency to an interspersal which is only expressed fully in Pinus. In the soft pines eleven out of thirteen species show, as a rule, as in the previous genera, that the tracheids are rarely interspersed, *P. aristata* forming a partial exception, as shown in a sparing interspersal. *P. monophylla* and *P. monticola*, on the other hand, show a strong interspersal of the tracheids, and in this respect they approach the hard pines. In the latter group we again find the first four species characterized by a rare interspersal. But passing on to the more highly developed species, such types as *P. clausa*, *P. palustris* and *P.*

glabra show that the interspersed tracheids are not only numerous, but that they eventually become conspicuously predominant and often constitute the bulk of the ray structure. It is evident then that such features possess an evident value for diagnostic purposes, particularly in the genus Pinus where the variations are numerous, well defined, and applicable to particular species or groups of species.

Tangential Section.— As displayed in tangential section, the medullary ray exhibits two principal forms, each of which presents features of great taxonomic and phylogenetic value. The type of structure which prevails, and which may be regarded as the fundamental form of the ray, is that of from one to many cells superimposed in a single series of varying height (Fig. 25). Such uniseriate rays are characteristic features of all the investigated recent genera. In 30 % of the genera, there is a sporadic tendency to a multiseriate form as expressed in the development of rays which are 2-seriate in part. Such enlargement is not confined to any particular portion of the structure, and within the limits of the same section it may arise at the centre or at either end. It is never found in Abies, Picea or Pinus, but it is met with in *Pseudotsuga macrocarpa*, three species of Cupressus, two of Juniperus, one each of Sequoia and Araucaria and two of Larix (Fig. 26). In Libocedrus such tendency is much more pronounced, and the rays may be described as 2–3-seriate in part.

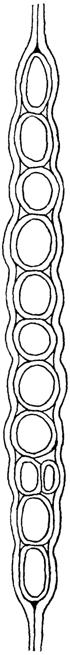


FIG. 25.— *Sequoia sempervirens.* Tangential section of a medullary ray showing a typically 1-seriate ray of broad form. × 280.

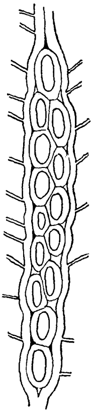


FIG. 26.— *Taxus brevifolia* Tangential view of a medullary ray, showing its 2-seriate character. × 280.

This feature is of so sporadic a nature that existing species afford no satisfactory evidence as to its origin or significance, but reference to Cordaites tends to throw some light upon this somewhat obscure problem. In fourteen species of Cordaites, three of which are European (25, p. 606–609) it is seen that the rays present four variants ranging from the strictly uniseriate form to 1–2-, rarely 3-seriate. The distribution is in the following percentage proportions:

1–2-, rarely 3-seriate	21.4 %
1–2-seriate	14.3 %
2-seriate in part	50.0 %
1-seriate	14.3 %

From this it would appear that Cordaites as a whole, approaches the primitive, multiseriate ray such as may be found in the Cycads, much more nearly than any of the existing species under consideration, and from this point of view it becomes possible to arrange a sequence showing the relative development in the following terms: (1) Cordaites, (2) Libocedrus, (3) all other genera as enumerated above. The evidence of fossil plants, however, shows that caution must be exercised in our estimate of what constitutes the primitive ray. The structure of Stigmaria shows a preponderance of uniseriate medullary rays (51, p. 224) and that such are primitive rays cannot well be doubted. In general, however, we are probably not far from correct in the assumption that the highest form of the ray is expressed in its uniseriate character. Deviations from this would then require to be interpreted as vestigial features which indicate a relatively lower type of organization in direct proportion to the increase of a tendency toward a multiseriate form.

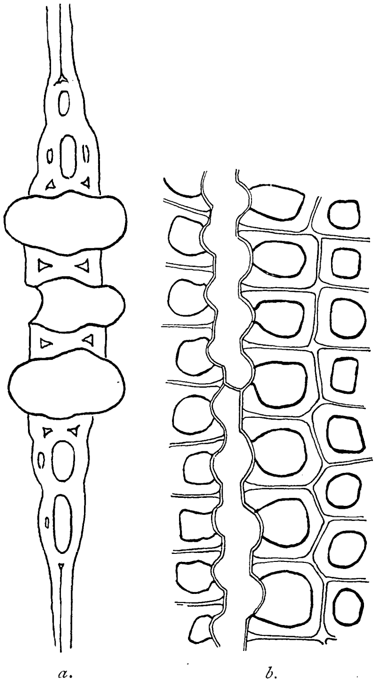


FIG. 27.—*Pinus reflexa.* (*a*) Tangential section of a medullary ray, showing the typically inflated cells. × 420. (*b*) Transverse section of a medullary ray, showing the inflation of the cells opposite tracheids. × 300.

In the majority of species, the side walls of the parenchyma cells are thick and traversed by small pits. In the genus Pinus the wall is commonly thin and it closes the orifice of a very large pit on the wall of the adjacent wood tracheid. This is notably true of the soft pines in which the side wall either projects as a convex membrane, or it is concave and curves into the cell cavity. Such a feature is of very little if any importance with the exception *P. reflexa*, in which the thin side walls almost invariably project so as to give the cells a correspondingly inflated appearance (Fig. 27*a*). It is not only apparent in a tangential section, but it is very conspicuous in the transverse section (Fig. 27*b*) where the inflated walls are seen to project into the cavities of adjacent wood tracheids, thereby giving to the ray a beaded appearance. As an exceptional variation it possesses no apparent significance with respect to questions of descent.

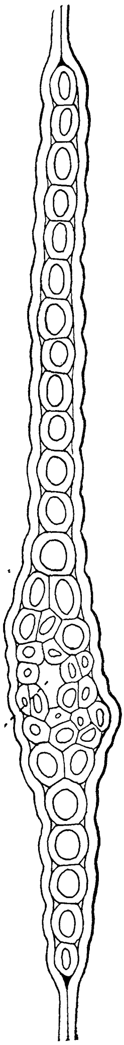
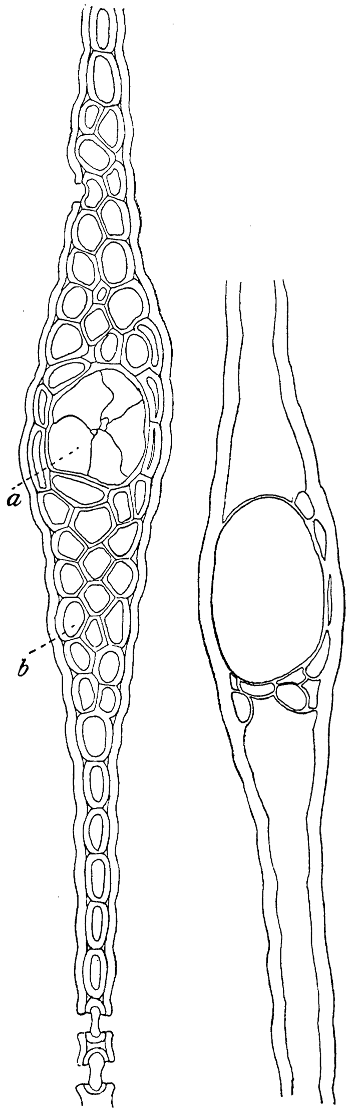


FIG. 28.—*Pseudotsuga douglasii.* Tangential section of a fusiform ray showing (*a*) the typical resin canal with thick-walled epithelium, but devoid of thyloses. × 280.

The second form of the ray is that which has been designated as fusiform in reference to its characteristic outline (39). Such rays occur in relatively few of the existing genera to the extent of 20 %. They occur typically in Pseudotsuga, Larix, Picea and Pinus, and they are thus seen to be characteristic of the most advanced types. Among extinct species they are unknown except in the case of *Sequoia burgessii*[1] (41, 42–46) in which they present a remarkable exception to the general course of development and structure of that genus. The fusiform rays are peculiar in their structural features. They vary greatly in height as between different genera, and such variations also occur within a given genus, the extremes being met with in the genus Pinus, where *P. palustris* and *P. ponderosa* present the antithetic relations. In most cases they are much higher than the uniseriate rays with which they are associated, but this rule is subject to several exceptions. They are always distinguished by a broadening of the central tract by two to several times the original dimensions, thereby becoming more or less multiseriate. These variations depend upon the nature of the included structure which exhibits modifications directly related to progressive development of the genus. Such broadening arises abruptly in Pseudotsuga, Larix and Picea, so that the terminals above and below consist of a single series of cells with the general structure of the uniseriate ray (Fig. 28). In Pinus the broadening is less abrupt, diminishing in both directions somewhat gradually, thus giving rise to a region of lenticular form, which occupies upwards of half the height of the ray, or in some cases constitutes the entire structure. From this it follows that in such types as *P. palustris* (Fig. 29*b*), the terminals which are often prolonged to great length, may be linear and uniseriate, while in *P. clausa* the whole ray is lenticular in outline and the terminals consist of only one or two limiting tracheids (Fig. 30). Within the region of the central tract the cells are all thick-walled in Pseudotsuga, Larix and Picea, but in Pinus the cells are generally thin-

---

[1] Dr. E. C. Jeffrey has recently discovered the same feature in another extinct Sequoia now in course of publication.



a. *b.*

FIG. 29a.—*Pinus albicaulis.* Tangential section of a fusiform ray showing a typical resin canal with (*a*) thyloses, and (*b*) rather thick-walled parenchyma. × 280.

b.—*Pinus palustris.* Tangential section of a fusiform ray in part, showing thin-walled parenchyma broken out. × 280.

walled, and in the hard pines this feature is emphasized by a degeneration of the tissue to such an extent that it is readily broken out in making sections, whence it characteristically appears either much broken up or entirely wanting. The principal feature of such rays, and the one which determines their form, is the presence of a resin canal in each case. Such resin canals traverse the ray continuously for its entire length. They present the same details of structure as the resin canals which lie within the xylem. In Pseudotsuga, Larix and Picea, the central canal is narrow, especially in the first two genera, and the epithelium consists of a single layer of thick-walled cells. In Pseudotsuga and Larix (Fig. 28), thyloses are altogether wanting, but in Picea they are of sporadic occurrence. In Pinus (Figs. 29 and 30) on the contrary the canals are always distinguished by their great breadth; the epithelium is composed of one to several rows of thin-walled cells which are often resinous and often much disorganized, while thyloses are an invariable feature of the central canal.

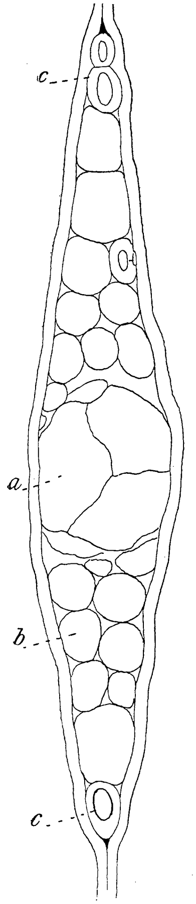


FIG. 30.—*Pinus clausa.* Fusiform ray showing (*a*) the resin canal with thyloses, (*b*) thin-walled parenchyma cells and (*c*) the terminals composed of only one or two tracheids. × 280.

A comparison of different genera and species shows that there is a somewhat striking variation in the number of uniseriate rays (tangential) to a given area of section. Such variations may arise within narrow limits in the same species according to location and conditions of growth, but apart from this there are somewhat constant variations between different species which may be expressed by the use of the relative terms few, many. No attempt has been made to define such variations and more exactly, but it is quite possible that a determination of the average number to a square centimeter, or other convenient unit, might disclose a somewhat greater differential value than is at present apparent. A simple illustration will serve to afford an idea of the rather limited specific value of this character. In *Taxus cuspidata* the rays are numerous, while in the two remaining species they are relatively few. The same feature applies to the differentiation of *Torreya nucifera* from the other species of that genus. In *Pinus clausa*, *P. serotina*, *P. murrayana*, etc., the same rule applies, but in all such cases it cannot be accepted as final.

The height of the ray is subject to such variations, even within the same species, that it cannot be defined with sufficient accuracy to admit of its application to classification in more than a very general sense. It is true that the rays of Ginkgo are always low, while those of Taxus and Torreya are often high. In Juniperus they are commonly low, while in Pinus they range from low to very high. Such variations do not possess sufficient constancy to admit of either generic or specific application in the strict sense, though they not infrequently serve a useful purpose as controlling factors, and they are therefore incorporated in all the diagnoses. Variations in breadth have a much more definite value, since the element of constancy is well defined. The genus Thuya (Fig. 31) may almost invariably be differentiated by this feature. In Cupressus, *C. thyoides* may be distinguished by a similar feature, while *C. arizonica* and *C. goveniana* are equally well indicated by the great breadth of the rays. The same rule applies also to Juniperus, Sequoia (Fig. 25), Pinus, and other genera, whence it appears that this feature is of specific value. It is always associated with and dependent upon the form of the component cells (tangential) which afford a means of distinguishing genera and species with much directness. The narrowly oblong cells of Thuya (Fig. 31) serve to separate this genus without difficulty, since a similar feature occurs but rarely elsewhere, and then in such association as to make the differentiation clear. In Juniperus the genus is separable into

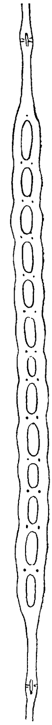


FIG. 31.—*Thuya gigantea*. Tangential section of a ray, showing the typically narrow and oblong cells. × 280.

four well marked divisions: (1) round to oval or transversely oval; (2) rays broad, the cells oval to round, chiefly round; (3) chiefly oval, and (4) rays narrow, the cells oblong to oval, chiefly oblong. The broadly oval and thin-walled cells of Sequoia separate it from associated genera. In Picea the genus may be subdivided accordingly as the cells are (1) variable, round, oval or oblong; (2) equal and uniform, oblong or oval.[1] Capressus is similarly separable into groups. But more specifically it is not difficult to separate *C. arizonica* and *C. goveniana* by reason of their broad rays and very conspicuously transversely oval cells, from *C. pisifera* with its round or oval cells and *C. thyoides* with its narrow, oblong, rarely oval cells. In the genus Pinus attention is at once directed to *P. murrayana* by the conspicuously round or transversely oval, very unequal and variable cells.

The interspersal of the tracheids often imparts a characteristic appearance to the tangential aspect of the ray, especially in the genus Pinus, and more particularly among the hard pines. In this group the tracheids present very variable forms and sizes. In such types as *P. glabra* they are small, oval or round, and wherever they occur they give rise to a marked local contraction. In *P. palustris* and *P. cubensis* they are commonly oblong and not infrequently they become several times higher than broad. As they are almost invariably narrower than the associated parenchyma cells, they cause a local contraction which sometimes extends over considerable distances. In *P. palustris* the predominance of the tracheids is carried so far that the rays are chiefly composed of them, and it then becomes appropriate to apply the term interspersed to the few parenchyma cells. In all of the more highly organized rays of the hard pines the appearance of the structure is so complex and variable that a proper diagnosis can be drawn only when we take cognizance of the principal aspects presented, and these sometimes amount to as many as four in number.

A consideration of the various structural features thus discussed in their relations to classification will show that no other portion of the stem possesses so many elements of importance as the medullary ray which, in consequence, attains the highest value in this respect and affords differential characters of wide range, great prominence, easy recognition and of primary importance in the differentiation of groups, genera and species; and as a general summary, the utility of these characters for such purposes is approximately indicated in the following tabulation:

---

[1] The term equal here applies to cells of the same ray which are of the same width; uniform to the cells of all rays which are pretty constantly of one form; the contrasting terms being unequal and variable respectively.

1 Rays (tangential) of two kinds.
2 Ray tracheids.
3 Pits on the lateral walls of the ray cells simple or bordered.
4 Terminal walls of the ray cells thin and entire or locally thickened. } Generic.
5 Form and character of the ray cell (tang.)
6 Form and size of pits on the lateral walls of ray cells.
7 Ray tracheids dentate or reticulated.

8 Direction and form of orifice of pits on the lateral walls of ray cells. } Specific.
9 Upper and lower walls of ray cells.
10 Ray tracheids interspersed or marginal.
11 Disposition of pits (radial).
12 The number of pits per tracheid.

THE RELATIONS OF MEDULLARY RAYS TO DEVELOPMENT.

We are now in a position to determine the relations in which the various structural features of the medullary ray stand to development, and for this purpose it may be most convenient to discuss them in that sequence which is apparently consonant with the general order of evolution of the entire group.

It has been ascertained that bordered pits are characteristic features of the lateral walls of the ray cell in 72.4 % of the investigated species, and that in the remaining 27.6 % among the higher types, simple pits predominate, but a closer scrutiny of this latter group discloses some features of more than passing interest. Reference to the table of anatomical data will show that the change from bordered to simple pits is entirely confined to the genus Pinus, and that it does not rise abruptly as if in response to some unusual condition whereby a profound alteration in the usual course of development was induced ; but it is effected by stages, showing that whatever influences were brought to bear, they operated gradually through a somewhat prolonged period of development, while here and there strong tendencies to reversion were manifested, and that the alteration was finally effected in a permanent way, only in the most highly developed pines. Commencing with *P. lambertiana* it will be observed that some species of the soft pines are characterized by simple pits. Among the hard pines *P. clausa* and *P. rigida* have bordered pits, while the six following species again show simple pits. We next come to a group of four species, with one exception (*P. murrayana*) Japanese, in which there is a mingling of both bordered and simple pits, showing a decided persistency of the primitive character in the face of conditions which involve a change. Following these are two species with simple pits, one with transitional features, five with simple pits, one with bordered pits, one with the transitional form and the remaining six species with simple pits, only. It will therefore be seen that these changes occur in waves, and that within the limits of forty-one species there are three complete and six incomplete recurrent phases. If we were arguing from purely theoretical grounds, all of these species should be arranged in such order as to show, (1) bordered pits, (2) transitional forms and (3) wholly simple pits, and we should thereby gain a perfect, developmental sequence. But such a position would not be justified by other evidence of an equally, if not more weighty character, and it is our object to interpret the facts as they are found. It has already been shown that the occurrence of simple pits in the pines is consonant with a higher type of development, and that the change is not only accompanied by sporadic reversions or survivals as one may choose to regard them, but that the change as a whole is a process of reduction. From this point of view then, we must regard the occurrence of bordered pits in *P. clausa*, *P. rigida* and *P. pungens* as pure survivals of a more primitive structure, a feature which is less perfectly expressed in such transitional forms as *P. koraiensis* or *P. inops*. But a mere mingling of the two kinds of pits in the same species is not the only evidence in this direction. The mingling of simple and bordered pits does not occur indiscriminately, but in accordance with a well defined law to the effect that the former are characteristic of the spring wood throughout its entire extent, while the latter occur only in the summer wood where they might be expected if at all, since the arrested development which might be complete in the case of relatively thin-walled cells, could be readily overcome in part, in walls of greater secondary growth. This in no way conflicts with the observed fact that in the majority of cases, the usual course of development is such that the bordered pits of the spring wood very commonly become reduced to simple pits in the summer wood in accordance with De Bary's law as already stated in application to other cases. Constancy in the structure of such pits has been found to be characteristic of Cordaites, Ginkgo, the Taxaceæ and all the lower forms of the Coniferæ, from which we may conclude that the bordered pit is essentially a primitive character. On the other hand variation is a well marked feature of the pit in the genus Pinus as first expressed in the large, oval or squarish and open pits of *P. resinosa* or *P. thunbergii*, and as later appears with greater frequency in the smaller and very inconstant pits of *P. tæda* or *P. palustris*. Such variations then, involving a gradual and complete transformation to the condition of simple pits, are characteristic only of the more highly developed pines, from which it may be concluded that it is a feature consistent with a relatively high order of development in exact accord with the principles governing parallel changes in the pits of the wood tracheids. They are also in harmony with the well-known principle that variation is always of a more simplified form in primitive types, but that it tends to greater diversification with advance in organization and general development, as a necessary sequence to the adjustment of the organism to a wider and more complex environment. Finally it has been shown that the elimination of the bordered pit proceeds concurrently with the more complete organization of the ray tracheids, in response to a substitution of functional activities between these structures and the degenerate parenchyma cells. We may therefore conclude that extreme variation in the character of the pit is an expression of a higher type of development, and that from this standpoint, such structures have a definite value in solving questions of descent.

The terminal walls of the ray cells present three variants with respect to secondary growth. All the more primitive Cordaitales and Coniferales are characterized by thin walls. Cupressus and Juniperus are chiefly distinguished by their thin walls which are also locally thickened, a feature which has been shown to be due to incipient secondary growth. But such alterations are already foreshadowed in Libocedrus where the local thickening of the wall is of a sporadic nature. In *Abies magnifica* and *A. grandis* there is a partial recurrence of thin and locally thickened walls, which is pretty fully expressed in *A. concolor*. A similar recurrence is met with in *Pseudotsuga macrocarpa*, in *Picea polita* and in *Pinus parrayana*, and it is also complete in thirteen of the most highly developed species of Pinus, where the walls have suffered extreme degeneration. Within the limits of Picea (1) and the soft pines (5), there are six instances in all, of sporadic and partial survival of the thin and locally thickened wall. The first tendency to thick and strongly pitted walls is manifested in five species of Juniperus, and such development is fully expressed in what may be regarded as the three most highly developed species. Thick walls are then fully characteristic of Abies — with a partial reversion in *A. concolor*, of Tsuga, *Pseudotsuga douglasii*, Picea, with the exception of *P. polita*, five species of soft pines and three species of hard pines. In *P. tæda* and *P. palustris* the walls are so degenerate that their structure cannot be satisfactorily determined, but they are presumably thin-walled.

From these facts it is manifest that the progressive thickening of the terminal walls accords with the general course of development, and once more making use of the principles already applied to the pits on the lateral walls, we are brought to the natural conclusion that (1) an increase in the thickness of the walls is evidence of a higher type of organization, and (2) that the sporadic recurrence of thin walls with local thickenings represents the persistence of a primitive character.

Ray tracheids probably constitute one of the most valuable of the structural elements as an indication of development. This has its foundation (1) in the fact, previously shown, that they arise as secondary structures from the parenchyma elements, with which they exhibit interchangeable relations, in direct response to the requirements of a higher degree of organization, and (2) their general relation to progressive development. The complete absence of ray tracheids from the Cordaitales and Ginkgoales, as also from the Taxaceæ and more primitive Coniferæ, while they are invariable features of the higher Coniferæ in which they attain their most complete development, admits of only one interpretation. The fact that they are exclusive features of the Coniferæ emphasizes their inferior value for determining the derivation of that group, while it points to their superior importance as a factor in the sequence of the various coniferous genera. They occur sporadically in Thuya (1), Cupressus (2), Juniperus (1), and Abies (1). They are prominent features of Tsuga, Pseudotsuga, Larix, Picea and Pinus. Their invariable absence from Sequoia would appear to suggest that this genus is more primitive than Thuya, but there are other reasons which serve to suggest the opposite relation. Apart from this exception it will be seen that in accordance with the relations exhibited in the table of anatomical data, the genera enumerated form a continuous series, commencing with those showing sporadic tracheids, and ending with those in which such structures attain their highest expression. From this we are justified in the conclusion that the rare occurrence of tracheids in Thuya, etc., is to be interpreted as the first evidence of a tendency in development which is only fully realized at a later period, and this appears to be justified by a closer examination of the last five genera in this respect, since it is found that in them the tracheids not only show a progressive numerical development, but their structure likewise becomes more complicated in direct relation to the evolution of higher types of genera and species. We must therefore look upon the tracheids, with their thin, simple walls, as the primitive form, while those with the strongest reticulations are of the highest type, the two being united by a transitional form characterized by the presence of simple teeth. The evidence at hand does not appear to justify the idea that the various genera have been segregated into small groups representing side lines of development, but it rather favors the thought that each genus is in itself a complete, short line of descent, and that among these a prominent parallelism has arisen in the tendency toward the development of tracheids — a tendency which has been carried to completion in the case of only five of the series, and in such a way that in only a portion of one of these has that completion reached its highest expression.

The occurrence of two kinds of parenchyma ray cells is an exclusive feature of the genus Pinus, and their value for phylogenetic purposes is strictly confined to the relations of the various species of pines. The first appearance of this differentiation is among the soft pines in *P. aristata* and *P. edulis*. It is to be observed, however, that the thick-walled cells are always dominant, the thin-walled cells being interspersed among and coterminous with them. No further evidences of such structural alterations are to be noted until we reach the more highly developed representatives of the hard pines. Among these definite transition forms occur in *P. murrayana*, *P. coulteri*, *P. jeffreyi*, *P. virginiana*, *P. insignis* and *P. cubensis*, while in *P. arizonica*, *P. ponderosa*, *P. sabiniana*, *P. pungens*, etc., the original relations are exactly reversed and the thick-walled cells show a diminishing frequency, until in *P. glabra* and *P. tæda* they are rarely met with. Such facts give effective proof to the belief that structural alterations of this nature are not only evidences of the highest type of development among the pines, but in the Coniferales as a whole.

The invariable absence of the fusiform ray from all except the four genera which attain the highest structural development, and their constant occurrence in all the species of such genera, presents an argument of great force as showing their relation to the evolution of advanced types. There is here no evidence of sporadic development, foreshadowing the general course of evolution, but the fusiform rays with their resin canals appear abruptly and permanently. Among fossil plants — except the genus Pityoxylon which, being essentially Pinus, falls under the general rule — there is no instance of such structures outside of the four genera named, save in the case of the remarkable *Sequoia burgessii*, from the Lignite Tertiary (4, p. 242) and *S. penhallowii* of Jeffrey. As it will be necessary to further discuss the essential structure of the fusiform ray when considering the resin passages in particular, it will be unnecessary to deal with it more at length at the present moment.

Errata.

Page 249. For Cordaite*d* read Cordaite*s*.
Page 263, Fig. 12. For Radial read *Tangential.*

(*To be continued.*)